
AN UPDATE ON THE SYSTEMATICS AND OCCURRENCE OF THE FANWORM GENUS *PSEUDOFABRICIOLA* FITZHUGH, 1990 (POLYCHAETA: SABELLIDAE: FABRICIINAE) IN THE MEDITERRANEAN

KIRK FITZHUGH¹ AND NOMIKI SIMBOURA²

ABSTRACT. Fitzhugh et al. (1994) originally described *Pseudofabriciola analis* from the Adriatic Sea off Italy at a depth of 22 m and *P. longipyga* off the island of Lésvos in the northeast Aegean Sea at 21 m. Range extensions for both species are reported. *Pseudofabriciola analis* has been found in the Ionian Sea off the west coast of Greece at a depth of 15 m, and *P. longipyga* appears to be distributed throughout the Aegean Sea, having been found off the island of Rhodes (63–71 m), on the Cyclades Island plateau (112 m), and off Greece in the Saronikos Gulf (85 m). The description of *P. longipyga* is emended based on this additional material to include features of the branchial crown, which was originally unknown. Specimens also display varying degrees of contraction of anterior and posterior ends, which can result in body dimensions significantly differing from what was described for the types. Unlike the holotype and paratype of *P. longipyga*, all nontype specimens have equally developed pygidial eyes. Cladistic relationships of *P. longipyga* to other species in the genus are reassessed.

INTRODUCTION

Two fanworm species in the genus *Pseudofabriciola* Fitzhugh, 1990, *P. analis* and *P. longipyga*, were recently described by Fitzhugh et al. (1994). Both species are known only from the Mediterranean, with *P. analis* originally described from the Adriatic Sea off Brindisi, Italy, and *P. longipyga* from the northeast Aegean Sea off the island of Lésvos (Fig. 1). Additional specimens of both species have been made available to us through the National Centre for Marine Research, Greece, as a result of benthic surveys carried out in the Ionian and Aegean Seas. One of the objectives of the present paper is to present range extensions for both species based on this new material.

Pseudofabriciola longipyga was originally described from two specimens, both lacking a branchial crown. This species was first identified as *Fabricia filamentosa* (non Day, 1963) by Simboura (1990), who reported its occurrence off Lésvos (the type locality) and Rhodes. At the time they described *P. longipyga*, Fitzhugh et al. (1994: 229) considered the specimens from Rhodes to be a

separate, undescribed species. Subsequently, however, additional specimens of *Pseudofabriciola* have been recovered from other localities in the Aegean Sea, which exhibit a range of overlapping morphological variation sufficient to suggest that all are members of *P. longipyga*. We here present additions to the description of *P. longipyga* as well as a description of the branchial crown of this species. Cladistic relationships between this species and others in the genus are also reevaluated.

All specimens examined have been deposited in the Allan Hancock Foundation Polychaete Collection of the Natural History Museum of Los Angeles County (LACM-AHF).

SYSTEMATICS

Pseudofabriciola analis
Fitzhugh, Giangrande, and
Simboura, 1994

Fabricia filamentosa. Giangrande and Castelli, 1986: 119–122, fig. 1 (non Day, 1963); Giangrande, 1989: 163 (non Day, 1963).

Pseudofabriciola analis Fitzhugh, Giangrande, and Simboura, 1994: 221–226, figs. 2–5.

MATERIAL EXAMINED. Western Ionian Sea: west coast of Peloponissos Peninsula, depth 15 m, sandy silt, 24 July 1982; 14 specimens (LACM-AHF 1710).

1. Invertebrate Zoology Section, Research & Collections Branch, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, USA.

2. National Centre for Marine Research, Gr. 16604 Hellenikon, Athens, Greece.



Figure 1. Known occurrences of *Pseudofabriciola analis* (circles) and *P. longipyga* (squares). Type localities are indicated by an asterisk, other localities by diagonal lines.

REMARKS. All specimens are complete except for the branchial crown. Total body length ranges from 1.5 to 3.0 mm. The specimens agree well with the description of the species given by Fitzhugh et al. (1994). *Pseudofabriciola analis* is easily identified by the shallow, ventral anal depression on the pygidium (cf. Fitzhugh et al., 1994: fig. 4A, C) and especially the paired midventral lobes that border the anterior margin of the depression. Another important diagnostic feature is the arrangement of notches on the anterior peristomial ring collar. *Pseudofabriciola analis* has two pairs of dorsolateral notches but lacks a middorsal notch or incision (Table 1; cf. Fitzhugh et al., 1994: fig. 3C). The other five species with dorsolateral notches only have one pair, whereas two species lack notches altogether.

With respect to depth, the occurrence of *Pseudofabriciola analis* in the Ionian Sea is comparable to the depth (22 m) at which the types were collected and is consistent with the pattern of subtidal distribution recognized for most *Pseudofabriciola* species by Fitzhugh et al. (1994: 238–240, fig. 14). Similarly, the extension of the species' range from off southeastern Italy to the southwest coast of Greece is not surprising.

Pseudofabriciola longipyga

Fitzhugh, Giangrande, and Simbhora, 1994, emended

Figures 2–7

Fabricia filamentosa. Simbhora, 1990: 129–133 (non Day, 1963).

Pseudofabriciola longipyga Fitzhugh, Giangrande, and Simbhora, 1994: 226–230, figs. 6–7.

MATERIAL EXAMINED. **Southeast Aegean Sea:** Rhodes Island, depth 71 m, corallagenous substrate, August 1983, 7 specimens (LACM-AHF 1713, only 1 specimen with branchial crown); Rhodes Island, depth 63 m, muddy sand, February 1984, 7 specimens (LACM-AHF 1714, all lacking branchial crown). **South Aegean Sea:** Cyclades Island plateau, 37°18'30"N, 25°23'45"E, depth 112 m, muddy sand with detritus, September 1989, 2 specimens (LACM-AHF 1712, all lacking branchial crown). **Southwest Aegean Sea:** Saronikos Gulf, 37°48'00"N, 23°41'50"E, depth 85 m, muddy sand, 26 April 1990, 8 specimens (LACM-AHF 1711, all lacking branchial crown).

ADDITIONS TO THE DESCRIPTION. All specimens slender, elongate. Total body length (ex-

Table 1. Comparisons of the principal features among described *Pseudofabriziola* species.

Species	Dorsal lips	Ventral filamentous appendages	Middorsal collar surface	Middorsal collar notch	Dorsolateral notches
<i>P. analis</i>	Narrow ridge	Absent	Smooth	Absent	Two pairs
<i>P. australiensis</i>	Unknown	Unknown	Smooth	Present	One pair
<i>P. californica</i>	Triangular lobe	Absent	Grooved	Absent	Absent
<i>P. capensis</i>	Triangular lobe	Absent	Grooved	Absent	One pair
<i>P. filamentosa</i>	Unknown	Absent	Smooth	Absent	One pair
<i>P. incisura</i>	Triangular lobe	Present	Smooth	Present	One pair
<i>P. longa</i>	Narrow ridge	Absent	Smooth	Absent	Absent
<i>P. longipyga</i>	Narrow ridge	Absent	Smooth	Present	One pair

clusive of branchial crown) from 2.1 to 6.3 mm (Table 2). Specimen with branchial crown 4.0 mm long, crown comprising 1.0 mm of this length. Crown with 3 pairs of radioles, each terminating to a filamentous tip; each radiole with 3–5 pairs of pinnules, all terminating at same height as radioles. Branchial lobes elongate, narrow (Fig. 5A), with attachment point to peristomium as a peduncle-like appendage. Dorsal lips low, broadly rounded ridges; ventral lips absent; ventral filamentous appendages absent. Anterior peristomial ring collar as

described by Fitzhugh et al. (1994; Figs. 2, 6), with narrow, V-shaped middorsal notch or incision and pair of shallow dorsolateral notches (Fig. 3A); one specimen with lateral collar margins distinctly uneven (Fig. 7), presumed to be a malformation. General dimensions of the anterior end of some specimens similar to the types, anterior end of other specimens can appear contracted or inflated to varying degrees. In extremely contracted specimens (Fig. 2), posterior peristomial ring and setigers 1 to 3 with broad dorsum, giving lateral margins of seti-

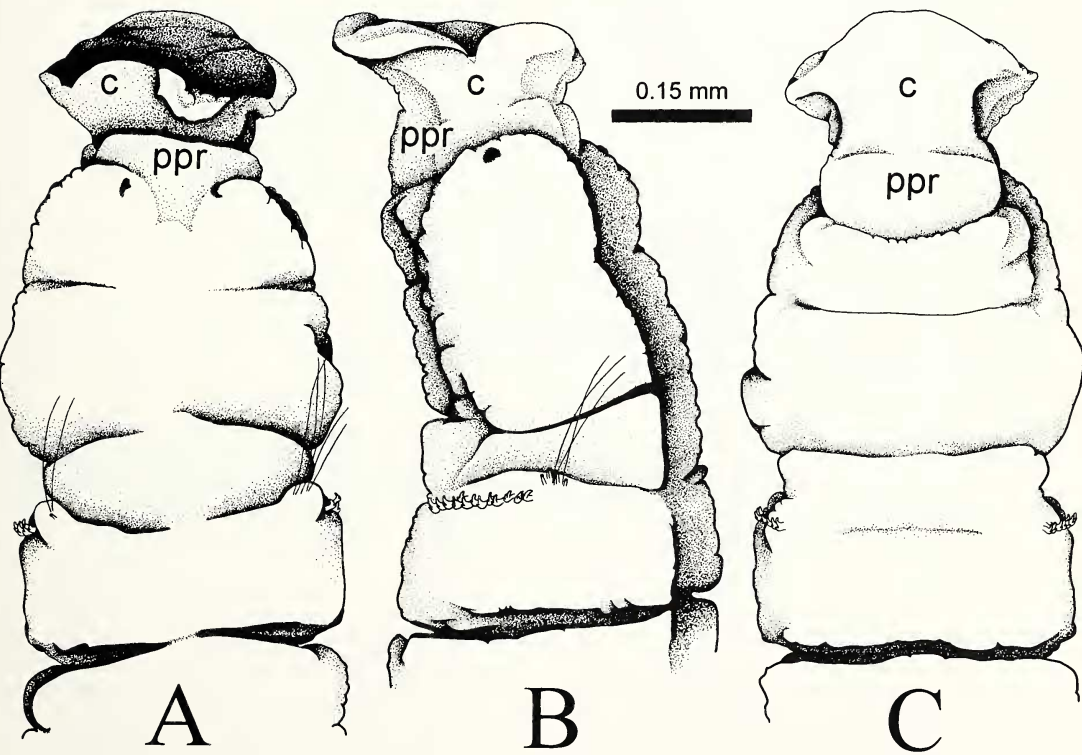


Figure 2. Anterior end of *Pseudofabriziola longipyga* (LACM-AHF 1714) from Rhodes. Note inflated, or swollen, state of setiger 1. A, dorsal view. B, lateral view, left side. C, ventral view. Abbreviations: c, anterior peristomial ring collar; ppr, posterior peristomial ring.

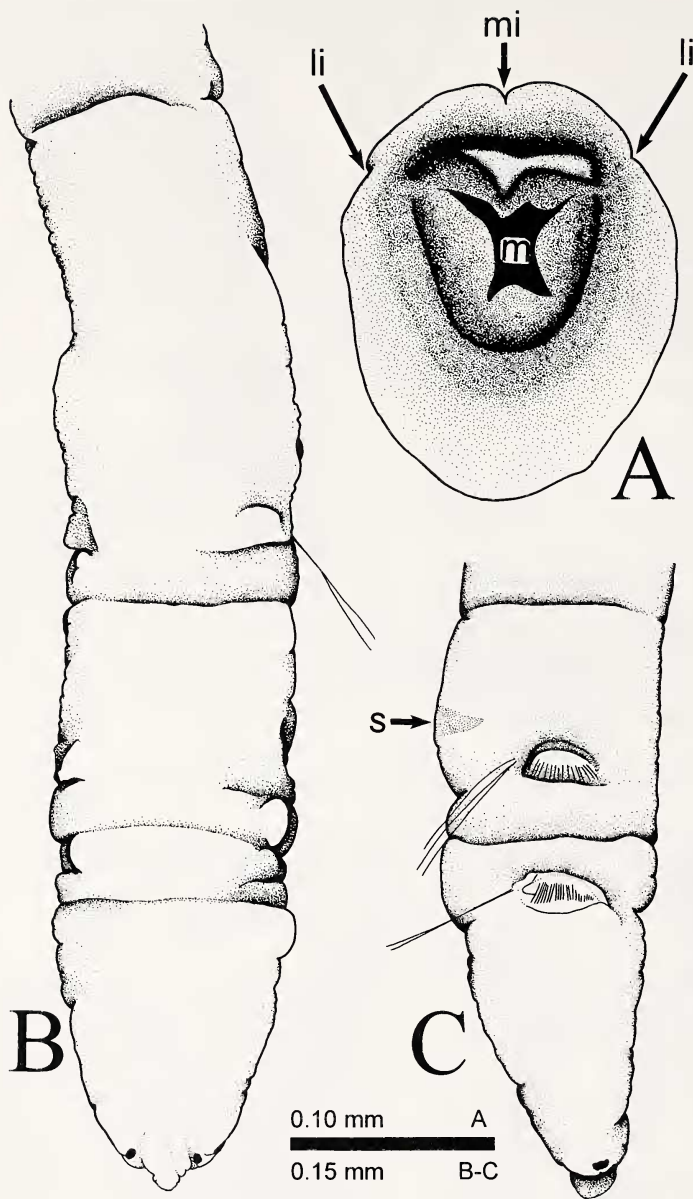


Figure 3. *Pseudofabriciola longipyga* (LACM-AHF 1714) from Rhodes. A, Head-on view of anterior end, branchial crown removed. B, abdominal setigers and pygidium, dorsal view. C, posterior end, left side, of specimen shown in B. Abbreviations: li, dorsolateral collar incision; m, mouth; mi, middorsal collar incision; s, swollen region on ventrum of setiger 10.

gers a distinctly swollen appearance. Ventrum of setiger 10 of most specimens with a low, rounded swelling as described in the types (Figs. 3C, 4A–B; e.g., Fitzhugh et al., 1994: fig. 1A, C); midventral surface of swelling with a single, or paired, opaque, roughly triangular patch (Fig. 4A), which extends into the body less than one-quarter of the width of the setiger (Figs. 3C, 4B). Some specimens with swelling and patch(es) indistinct, though area oc-

cupied by patch(es) more visible after specimen has been stained with methyl green. Paired pygidial eyes black or dark brown and equally developed (Figs. 3B–C, 4B, 5B). Pygidium shape variable, exhibiting three basic shapes: (1) narrow, very elongate condition seen in types (e.g., Fitzhugh et al., 1994: fig. 1A–C); (2) slightly longer than wide and more triangular (Fig. 5B); and (3) nearly as wide as long, posterior margin broadly rounded, with a small,

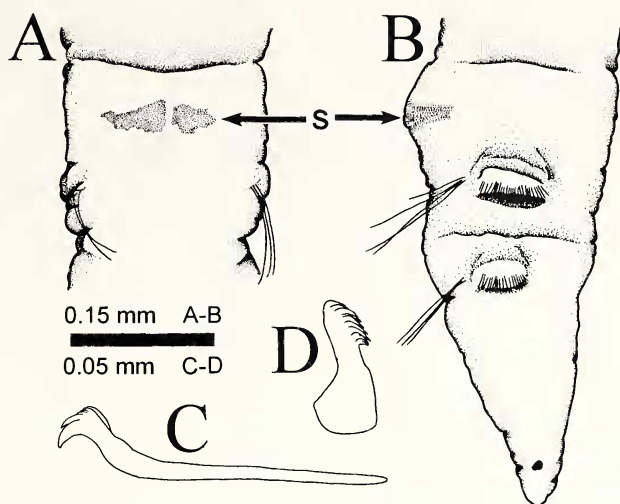


Figure 4. *Pseudofabriziola longipyga* (LACM-AHF 1714) from Rhodes. A, setiger 10, ventral view. B, posterior end, left side, of specimen shown in A. C, thoracic uncinus from setiger 4. D, abdominal uncinus from setiger 9. Abbreviation: s, swollen region on ventrum of setiger 10.

blunt caudal-like appendage between the pygidial eyes (Fig. 3B–C). Thoracic uncini acicular (Fig. 4C), teeth above main fang gradually decreasing in size, hood present. Abdominal uncini (Fig. 4D) with 8–9 rows of teeth, 2–4 teeth per row; manubrium slightly constricted below dentate region and 1.5–2 times longer than dentate region. Some specimens from Rhodes with light brown pigmentation in middorsal region of collar and anterior middorsal margin of posterior peristomial ring. Tubes composed of fine mud, some foraminiferan tests. No brooding of young observed.

REMARKS. In comparison to the types, the specimens described here show a range of variation in the anterior end and pygidium. These differences among specimens appear to be due to varying degrees of contraction as a result of fixation. The most

notable divergence from the types that does not appear to be a preservation artifact is in the pygidial eyes. Fitzhugh et al. (1994: fig. 6B–C) reported that both the holotype and paratype have a well-developed right eye and a left eye consisting of a group of small, dispersed eyespots. All specimens examined here have pygidial eyes equally developed. We have, however, chosen to place these specimens in *Pseudofabriziola longipyga* primarily on the basis

Table 2. Total body length (in millimeters), exclusive of branchial crown, of complete *Pseudofabriziola longipyga* specimens examined, and mean body lengths from each area.

Rhodes		Saronikos Gulf	Cyclades Island plateau
Sta. R1	Sta. R3		
2.1	3.5	3.4	2.3
2.3	4.0	3.6	2.5
2.3	4.0	3.6	
2.4	5.0	4.2	
2.5	5.3	4.3	
3.0	5.5	4.6	
3.2	6.3		
$\bar{x} = 2.5$	$\bar{x} = 4.8$	$\bar{x} = 3.9$	$\bar{x} = 2.4$

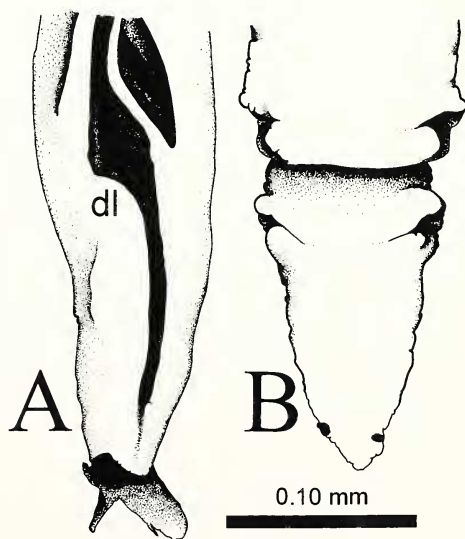


Figure 5. *Pseudofabriziola longipyga* (LACM-AHF 1713) from Rhodes. A, inner margin of left half of branchial crown. B, posterior end, dorsal view. Abbreviation: dl, dorsal lip.

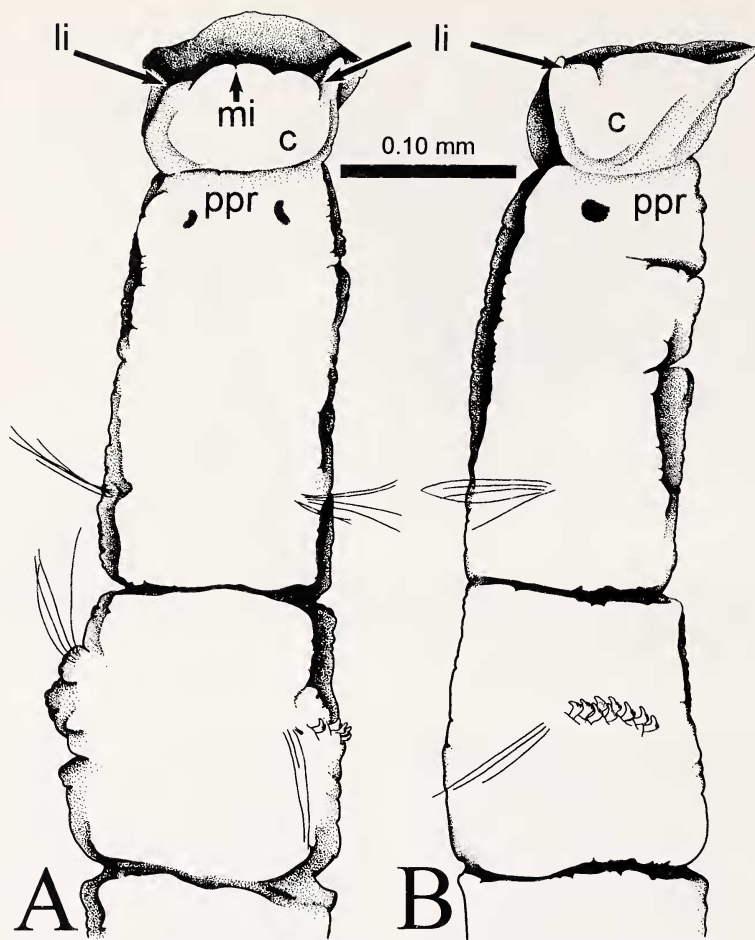


Figure 6. Anterior end of *Pseudofabriciola longipyga* (LACM-AHF 1713) from Rhodes. **A**, dorsal view. **B**, lateral view, right side. Abbreviations: c, anterior peristomial ring collar; li, dorsolateral collar incision; mi, middorsal collar incision; ppr, posterior peristomial ring.

of similarities in collar construction and setal types and the occurrence of the midventral swelling on setiger 10. Ideally, more material from the type locality is required to determine the consistency of pygidial eye development in this species.

The branchial crown of *Pseudofabriciola longipyga* is similar to that of *P. longa* and *P. analis* in that the dorsal lips are represented by low, narrow ridges (Table 1), in contrast to the plesiomorphic condition in which the lips are erect, triangular processes. These species differ in that the collar margin in *P. analis* has two pairs of dorsolateral incisions, while *P. longipyga* has only one pair and *P. longa* lacks incisions on the collar.

Pseudofabriciola longipyga appears to be a widespread species in the Aegean Sea. The known depth range for the species is now 21 (for the types) to 112 m. Simboura (1990) reported the occurrence of *P. longipyga* (as *Fabricia filamentosa* Day) from the vicinity of the type locality (Geras Gulf, Lésvos Island) at depths ranging from 6 to 21 m. Unfortunately, we cannot confirm these depth records

because the specimens no longer exist (Fitzhugh et al., 1994: 229).

RELATIONSHIP OF *PSEUDOFABRICIOLA LONGIPYGA* TO OTHER SPECIES IN THE GENUS

Analyses of the cladistic relationships among *Pseudofabriciola* species have been performed by Fitzhugh (1991a; see also Fitzhugh, 1991b, 1992, 1993) and Fitzhugh et al. (1994). The latter study included *P. longipyga*, but data on the branchial crown were lacking because only the types were used. A further consideration of the relationship of this species to others in the genus is presented here.

CHARACTERS AND CLADISTIC ANALYSIS

The nine characters used in the present analysis (Table 3) are the same as those used by Fitzhugh et al. (1994: table 1). In addition to the inclusion

Table 3. Characters and states used to determine cladistic relationships among *Pseudofabriciola* species. State 0 is plesiomorphic based on outgroup comparisons.

- 1. Dorsal lips: (0) well-developed, triangular lobe; (1) low, narrow ridge.
- 2. Branchial lobe shape: (0) wide and short; (1) narrow and elongate, and/or with a peduncle-like process.
- 3. Anterior peristomial ring collar: (0) low ridge or membrane; (1) high, with even sides; (2) high, with flaring sides.
- 4. Middorsal collar condition: (0) separate; (1) entire and distinctly grooved; (2) entire and smooth.
- 5. Middorsal collar margin: (0) separate; (1) entire; (2) notched or incised.
- 6. Dorsolateral incisions on collar margin: (0) absent; (1) present.
- 7. Thoracic uncini main fang: (0) slender; (1) swollen.
- 8. Thoracic uncini dentition: (0) large tooth above main fang; (1) series of subequal teeth above main fang.
- 9. Abdominal uncini manubrium: (0) about 1.5 times longer than dentate region; (1) about 2 times longer than dentate region; (2) about same length as dentate region.

of branchial crown data for *Pseudofabriciola longipyga*, several modifications were also made to states of characters 8 and 9 in the outgroup and *P. longipyga* (Table 4). Fitzhugh et al. considered the outgroup condition for character 8 (thoracic uncini dentition) to be state 0 (main fang surmounted by a large tooth and series of smaller teeth) and character 9 (manubrium length of abdominal uncini) to be state 0 (manubrium about 1.5 times longer than dentate region). Fitzhugh et al. (1994: fig. 1) based their coding of outgroup states on the relationship of *Pseudofabriciola* to other fabriciini genera as determined by Fitzhugh (1992; see also Fitzhugh, 1993). Subsequently, Fitzhugh (1995a: fig. 5) reported a much higher degree of ambiguity with regard to the relationship of *Pseudofabriciola* to other fabriciini, leaving open the question of plesiomorphic conditions for characters 8 and 9. As a result, these characters were coded as unknown (“?”) for the outgroup.

Minimum-length cladograms were produced

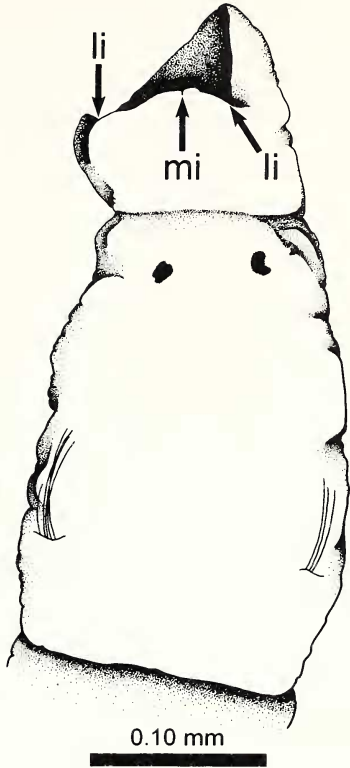


Figure 7. Anterior end of *Pseudofabriciola longipyga* (LACM-AHF 1712) from Cyclades Island plateau, dorsal view. Note deformation of collar. Abbreviations: li, dorsolateral collar incision; mi, middorsal collar incision.

from the data matrix (Table 4) using the *ie** command in Hennig86 (Farris, 1988). Multistate characters (3–5, 9) were treated as nonadditive, and no differential weighting was applied. Character-state changes were determined using Hennig86’s *xsteps* command with the *b* and *c* options.

Five trees were produced (Fig. 8), each with a length of 16 steps and consistency (ci) and retention (ri) indices of 0.81 and 0.76, respectively. Relation-

Table 4. Character-state matrix for *Pseudofabriciola* species based on character states presented in Table 3.

Characters	1	2	3	4	5	6	7	8	9
Outgroup	0	0	0	0	0	0	0	?	?
<i>P. analis</i>	1	1	2	2	1	1	0	1	2
<i>P. australiensis</i>	?	?	2	2	2	1	1	1	2
<i>P. californica</i>	0	1	1	1	1	0	0	0	0
<i>P. capensis</i>	0	1	1	1	1	1	0	0	2
<i>P. filamentosa</i>	?	1	1	2	1	1	0	1	1
<i>P. incisura</i>	0	1	2	2	2	1	1	1	2
<i>P. longa</i>	1	1	1	2	1	0	0	1	2
<i>P. longipyga</i>	1	1	2	2	2	1	0	1	1

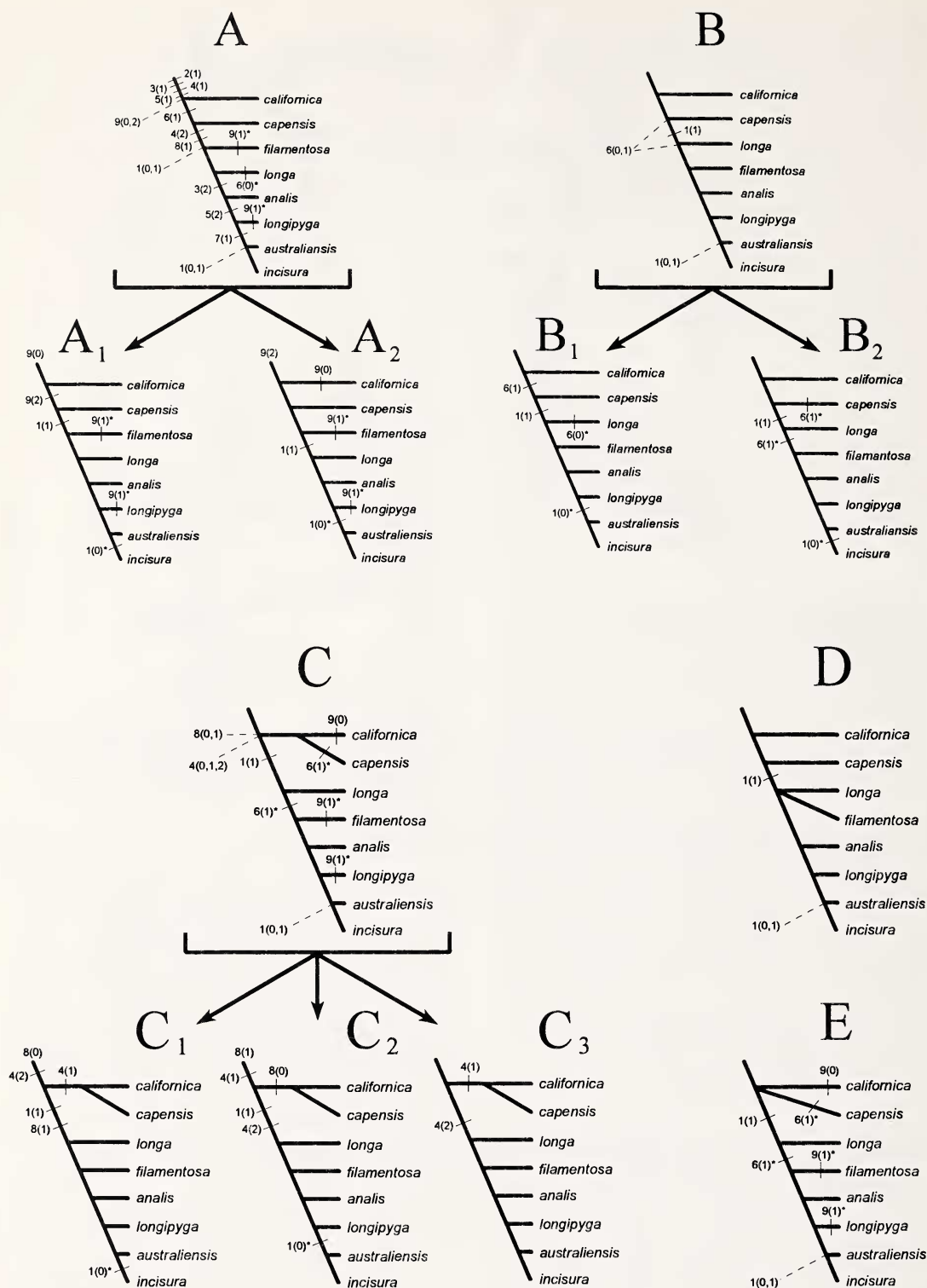


Figure 8. Minimum-length cladograms of *Pseudofabriciolo* species derived from the data matrix in Table 4. Length of each tree is 16 steps, $ci = 0.81$, $ri = 0.76$. Slashes on stems indicate character-state changes, with characters and states (in parentheses) indicated (cf. Tables 3 and 4). Homoplasious states are denoted by an asterisk. Ambiguous character-state changes are indicated at the nodes; trees A_{1-2} , B_{1-2} , and C_{1-3} show allowable transformation series for these characters. All character-state changes are shown in A; state changes in B-E are the same as in A except where indicated.

ships among four species, *Pseudofabricioloa incisura* Fitzhugh, 1990, *P. australiensis* (Hartmann-Schröder, 1981), *P. longipyga*, and *P. analis*, were constant among all trees and form an apomorphic clade relative to other species; this clade is defined by the peristomial ring collar being distally flared [character state 3(2); cf. Fig. 8A] as opposed to being of even width. *Pseudofabricioloa longa* Fitzhugh, 1990, and *P. filamentosa* (Day) are sister taxa to this clade and display three possible patterns of relationship (Fig. 8A–B, D), depending upon the transformation series of character 6 (dorsolateral collar incisions). *Pseudofabricioloa californica* Fitzhugh, 1991a, and *P. capensis* (Monro, 1937) are the most plesiomorphic species in the genus, with three trees (Fig. 8A–B, D) showing *P. californica* plesiomorphic to *P. capensis*, and other topologies with these species either as exclusive sister taxa (Fig. 8C) or forming a trichotomy with a clade comprising all other species (Fig. 8E). These topologies are mainly due to variations in transformation series in characters 4 (middorsal collar condition), 6, and 8 (thoracic uncini dentition). The greatest ambiguity in character-state transformation series within and among trees was in characters 1 (dorsal lip development), 6, and 9 (abdominal uncini manubrium length). These were the only characters that showed a ci and ri of less than 1.00; the ri of character 9 was 0.00.

DISCUSSION

Only two of the topologies (Fig. 8A–B) produced with the current data set are the same as those found by Fitzhugh et al. (1994: fig. 8A–B). Remaining trees from this latter study differ from the present results in that three of the eight trees contained the clade (*Pseudofabricioloa longa*, *P. filamentosa*, *P. analis*), and three trees had either the clade (*P. longa*, *P. filamentosa*) or (*P. longa*, *P. analis*). While a (*P. longa*, *P. filamentosa*) clade is consistent, though undefinable, with the topology in Figure 8D, an additional step (17 total) would be required to allow for the remaining clades.

The present study produced two topologies not reported by Fitzhugh et al. (1994), wherein *Pseudofabricioloa californica* and *P. capensis* form either an exclusive sister group (Fig. 8C) or a trichotomy with remaining species (Fig. 8E). Depending on the transformation series, the (*P. californica*, *P. capensis*) clade (Fig. 8C) can be defined by character 4 (middorsal collar condition; Fig. 8C₁, C₃) or 8 (thoracic uncini dentition; Fig. 8C₂). Since, however, the outgroup condition for character 8 was coded as unknown, either state 0 or 1 can be plesiomorphic for the genus. It is only when the plesiomorphic condition for the genus is state 1 (series of small teeth above the main fang) that the (*P. californica*, *P. capensis*) clade is defined by state 0 (presence of a large tooth above the main fang; Fig. 8C₂).

There are now only two species, *Pseudofabri-*

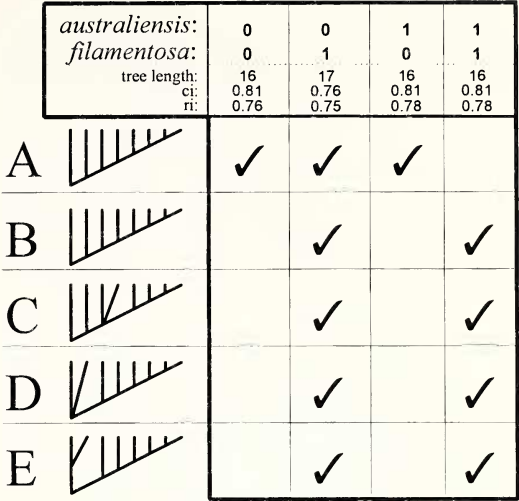


Figure 9. Possible tree topologies that result from each hypothetical combination of states for dorsal lip construction (character 1) in *Pseudofabricioloa australiensis* and *P. filamentosa*, as included in the data matrix in Table 4. Topologies are labelled to correspond to those in Figure 8.

cioloa australiensis and *P. filamentosa*, for which information on the branchial crown and dorsal lips (character 1) is lacking. Fitzhugh et al. (1994: fig. 10) presented the results of a series of cladistic analyses in which all possible combinations of states for character 1 might be encountered among *P. australiensis*, *P. filamentosa*, and *P. longipyga*. In those instances in which *P. longipyga* was coded with state 1 (dorsal lips as low ridges), topologies matched those presented here in Figure 8A–B and D. This sort of comparison is limited, however, given that the outgroup states for characters 8 and 9 have been modified for the present analysis. As an update to the simulations performed by Fitzhugh et al., we reanalyzed the possible resultant topologies that might occur once dorsal lip information is obtained for *P. australiensis* and *P. filamentosa*. The four data matrices derived from Table 4, which account for each of the possible combinations of states for character 1 that might occur in these two species (cf. Fig. 9), were analyzed using the Hennig86 commands described earlier. Two data sets produced single trees, each with a topology as in Figure 8A, and the other two data sets produced four and five trees, with topologies corresponding to Figure 8B–E and 8A–E, respectively.

Of the four possible combinations of dorsal lip states among *Pseudofabricioloa australiensis* and *P. filamentosa*, we predict that *P. australiensis* has state 0 (triangular lobe) and *P. filamentosa* has state 1 (low, narrow ridge). Under this prediction, the current data set still yields the five topologies in Figure 8A (cf. Fig. 9). *Pseudofabricioloa australiensis* closely resembles *P. incisura*, the latter having

triangular dorsal lips and ventral filamentous appendages (Table 1; Fitzhugh, 1990). All topologies in Figure 8 place these two species as exclusive sister taxa based on the main fang of thoracic uncini (character 7). An additional species from Belize, currently being described (Fitzhugh, in prep.), closely resembles *P. australiensis* and *P. filamentosa* in general collar construction and also has triangular dorsal lips and ventral filamentous appendages. Our prediction as to dorsal lip construction in *P. filamentosa* follows from the general observations by one of us (K.F.) that *Pseudofabriciola* species with very slender branchial crowns, such as *P. longipyga*, *P. analis*, and *P. longa* (Table 1), tend to have reduced dorsal lips. This pattern is also exhibited by another undescribed species from New Guinea (Fitzhugh, 1995b).

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NATURAL HISTORY MUSEUM
OF LOS ANGELES COUNTY
900 EXPOSITION BOULEVARD
LOS ANGELES, CALIFORNIA 90007